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Soil nutrients and microbial activity after early and late season prescribed burns in a Sierra Nevada mixed conifer forest

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ABSTRACT

Restoring the natural fire regime to forested systems that have experienced fire exclusion throughout the past century can be a challenge due to the heavy fuel loading conditions. Fire is being re-introduced to mixed conifer forests in the Sierra Nevada through both early season and late season prescribed burns, even though most fires historically occurred in the late season. We assessed the impact of early and late season prescribed fires on soil biogeochemical and microbiological parameters that are important for ecosystem recovery. We found that the late season burns had more dramatic short-term effects on soil abiotic conditions (temperature, moisture and pH), mineral soil carbon levels, total inorganic nitrogen, and microbial activity than the early season burns, relative to unburned sites, suggesting a higher severity burn. However, the total soil nitrogen pools and fluxes and soil respiration rates were not differentially impacted by burn season. These burn season effects suggest that soil variables may be regulated more strongly by fire severity than by the season in which the prescribed fire is conducted.

1. Introduction

Historically, fire has been an important driver of forest structure and composition for most forest ecosystems throughout the western United States (Covington and Moore, 1994). The common practice of fire exclusion during the first half of the 20th century has led to an increase in aboveground biomass and hazardous fuel levels (Covington and Sackett, 1984; Tilman et al., 2000; Schoennagel et al., 2004), leading to a shift in fire regime for many different forest types (Kilgore and Taylor, 1979; Swetnam and Baisan, 1996; Smith et al., 2005; Kaye et al., 2005; Smithwick et al., 2005). For the past few decades, land management agencies have employed prescribed burning to reduce these fuels and to restore ecosystem structure and function to pre-Euro-American settlement conditions. Prescribed fire can be difficult to employ, however, in systems that are far removed from their natural range of variability.

One example of a system that is far removed from its natural fire regime is the mid-elevation, mixed conifer forest of the southern Sierra Nevada of California. Historically, these forests experienced frequent (5–25 years), low severity fires during the mid-summer to early fall that maintained open stand structures and low fuel loads (Kilgore and Taylor, 1979; Miller and Urban, 2000; Keeley and Stephenson, 2000; Stephens and Collins, 2004). In many areas, prescribed burning has taken the place of these natural wildfires, but restoring fire regimes with fall prescribed burns alone is difficult. Fall prescribed burns are typically conducted after fuel moisture has dropped and weather variables have moderated but before the onset of late season storms. This leaves a narrow window for fall prescribed burning, limiting the number of acres that can be treated. In addition, stable atmospheric patterns typical of fall tend to restrict smoke dispersion, potentially impacting air quality in the neighboring Central Valley (Knapp et al., 2005). This region is plagued by poor air quality, so any activities that contribute to air pollution are highly controversial. Conducting prescribed burns earlier in the growing season when fuel moisture is higher and atmospheric conditions are more suitable for smoke dispersal is a potential solution, but the short- and long-term effects of early season burning on ecosystem processes and properties, such as biogeochemical cycling and soil microbial communities, are poorly understood.

Fire affects carbon cycling in forest soils directly by oxidizing many of the available compounds, and indirectly by changing environmental constraints on microbial activity. There are often

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short-term fire-induced changes in the nitrogen budget, as well. Soil inorganic nitrogen (NH_4^+ and NO_3^-) pools typically increase due to heat-induced NH_4^+ release from clay complexes (during fire), deposition of organic nitrogen in ash, enhanced ammonification rates (Grogan et al., 2000; MacKenzie et al., 2004), and, in some forest and prairie systems, nitrogen-fixation (by colonizing plants species post-fire) (Newland and DeLuca, 2000; Wan et al., 2001; Johnson et al., 2005; Smithwick et al., 2005). This pulse of available nitrogen has been shown to lead to short-term enhanced site productivity in systems that have experienced low intensity fire (Wan et al., 2001; Certini, 2005).

Season of fire may differentially impact the magnitude and direction of these biogeochemical effects through differences in fire intensity and differences in weather conditions immediately post-fire. Because fuel moisture in mixed-conifer forests of the Sierra is often greater in the early season, fuel consumption and the resulting intensity of such fires tends to be lower than with late season burns conducted under drier conditions. The temperatures reached during fire influence the chemical changes that dictate post-fire soil pH, moisture, nutrient concentrations (Choromanska and DeLuca, 2002; DeBano and Neary, 2005), and microbe and root survival (Dunn et al., 1985; DeBano and Neary, 2005). Therefore, season of fire may impact several components of belowground structure and function. Post-fire weather can also influence soil physiochemical conditions and nutrient concentrations. In the Sierra Nevada, the wet season typically runs between October and April, followed by dry summer months, with only one or two light rain events (Kilgore and Taylor, 1979). Heavy precipitation immediately after a burn can lead to a loss of the nutrient-rich ash layer through erosion and overland flow (Huffman et al., 2001). Consequently, because heavier fall and winter precipitation, in the form of both rain and snow, often occurs shortly after late season burns, post-fire nutrient loss may be greater. However, if there is sufficient snowfall immediately following the burn to stabilize the ash and remaining litter layer, there may be opportunity for the nutrients to be incorporated into the microbial biomass. These nutrients would then be released through mineralization throughout the winter or upon spring snowmelt, as has been shown to occur in mixed conifer forests (Williams et al., 1995; Miller et al., 2007) and other alpine systems (Williams et al., 1996; Kielland et al., 2006; Freppaz et al., 2007). Most of the trees were dormant during the late season burns but active during the early season burns. This difference could differentially impact their ability to capture nutrients immediately post-fire.

Recovery of soil nutrients post-fire is largely limited by microbial activity. One way to assess soil microbial activity is through soil enzyme analysis (Boerner et al., 2000). Soil enzymes reflect activities of microorganisms important for C, N, and P cycling (Sinsabaugh et al., 1993; Boerner et al., 2005). Two enzymes, acid phosphatase and phenol oxidase, represent the activity of important microbial functional groups involved in decomposition of labile and recalcitrant organic matter, respectively (Sinsabaugh et al., 1993; Carlisle and Watkinson, 1994; Boerner et al., 2000). Acid phosphatase is actively excreted by tree roots and microbial cells and passively released by ruptured cells. It is involved in P cycling in soils and is regulated by soil microclimate and organic carbon and phosphorus availability, with optimum activity at pH 5.0–5.5 (Saa et al., 1993). Phenol oxidase is a lignocellulose-degrading enzyme and is primarily limited by substrate and N availability (Boerner et al., 2005). It provides an approximate index of fungal activity (primarily white-rot fungi), which is important for breaking down large recalcitrant carbon compounds (Carlisle and Watkinson, 1994). The impact of fire on these enzymes and on the environmental factors that control their activity may help us understand the role of microorganisms in ecosystem recovery from disturbance.

Our objectives were to determine the short-term effects (1–3 years) of early and late season prescribed burning in a mid-elevation Sierra Nevada mixed conifer forest on (1) soil environmental conditions important for microbial activity (pH, moisture, temperature), (2) soil carbon and nitrogen pools and fluxes and (3) soil microbial activity.

2. Methods

2.1. Study sites

This project is part of the National Fire and Fire Surrogate Study (FFS), a nation-wide network of studies at 13 sites aimed at determining the effects of fuel reduction treatments on several ecosystem components, including vegetation, soils, insects, diseases, birds, and small mammals (Weatherspoon and McIver, 2000). This site was located within the watershed of the Marble Fork of the Kaweah River in the Giant Forest area of Sequoia National Park, California. The Mediterranean climate consists of cool, wet winters and warm, dry summers. Mean annual precipitation averages 114 cm, most of it falling as snow. The soils of this region have formed in residuum, colluvium and morainal material that have weathered from granitic rocks. They are classified as coarse-loamy, frigid Pachic Xerumbrepts (Huntington and Akeson, 1987). The dominant tree species in this mixed conifer, old growth forest are white fir (*Abies concolor* [Gordon & Glend.] Lindley), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), ponderosa pine (*Pinus ponderosa*), mountain dogwood (*Cornus nuttallii* Audubon), and California black oak (*Quercus kelloggii*). The sites we studied are all on west–northwest facing slopes of approximately 15–25° at elevations ranging from 1900 to 2150 m. The pre-settlement fire return interval, based on stem cross sections containing fire scars cut from snags in the study area was estimated to be 27 years (range = 7–56 years) (Schwilk et al., 2006). The last widespread fire in the study area occurred in 1879. The majority (89%) of fire scars were determined to be in the late wood or at the dormant ring boundary, indicating fires that burned primarily in the late summer and fall (Schwilk et al., 2006).

2.2. Sampling design and field measurements

Three replicate early season prescribed burn, late season prescribed burn, and unburned control sites were established in a completely randomized design, each averaging 15 ha in size of which the central 10 ha was used for data collection (see Fig. 1 in Knapp et al., 2007). The prescribed fires were conducted in September and October 2001 (late season) and June 2002 (early season) (see Table 1 and Knapp et al., 2005 for fire characteristics). This experimental design substitutes space for time (using data from control sites instead of pre-fire data), which is similar to other fire and restoration studies (LeDuc and Rothstein, 2007; Miesel et al., 2008), comparing treatments and reference controls within each year. Within each unit, ten modified Whittaker plots (50 m × 20 m) were installed at randomly selected gridpoints for vegetation sampling (shown in Fig. 1 of Knapp et al., 2007). In order to avoid disturbing the vegetation, we sampled soils 1 m outside the plots at each corner (four sub-samples per plot). We took soil cores (15 cm deep by 5 cm diameter) to assess nitrogen availability, soil moisture and pH in late season and control units in June 2002 (the next growing season after the late season burns), early season and control units in June 2003 (the next growing season after the early season burns), and in all units in June 2004. For nitrogen mineralization rates, we used the soil core incubation method, a modified version of the buried bag method (Raison et al.,

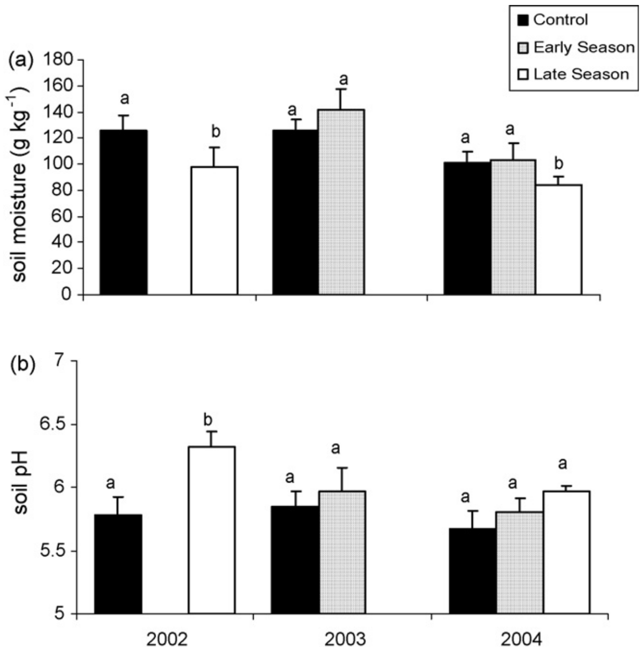

Fig. 1. Effects of early and late season fire on soil moisture (a) and pH (b) for each sampling year. Treatment means (+1 S.E.) are presented. Different letters denote a significant treatment difference ($p < 0.05$) for the given year.

1987; Hart et al., 1994). We collected one mineral soil sample for laboratory analysis (initial) and took another core adjacent to the first, placed it back into the soil with a perforated cap on the bottom of the core (to contain soil but allow for gas and water exchange), and replaced litter and duff layers. We returned 28 days later to collect the second soil core (final). At the time of removal, we immediately placed samples on ice and transferred them to the lab for same-day processing and KCl extraction. We calculated net nitrogen mineralization rate as the change in the total inorganic nitrogen concentration over the incubation time ((final–initial)/28 days).

We also collected and composited six mineral soil samples (four from each corner as for the N-mineralization work, plus two additional samples from the edge of the plot) for total C and N analysis and microbial enzyme analysis (2004 only). We measured soil respiration at all four corners of the subplots (2002 and 2003) and soil temperature at approximately 10 cm depth at two opposing corners (2004) using a PP-systems EGM-1 Soil Respirometer.

2.3. Laboratory analyses

We sieved soil samples through a 2 mm mesh within 12 h of collection and took 10 g sub-samples for moisture and pH. We determined soil moisture using the gravimetric method and soil pH using a 1:1 ratio of soil and de-ionized (DI) water. We dried and ground 10 g sub-samples of soil before measuring total soil C and N using a LECO CHN1000 combustion gas analyzer (LECO Corporation, St. Joseph, MI, USA). For nitrogen mineralization and nitrification rates, we extracted 10 g sub-samples in 50 ml 2 M KCl-PMA, filtered the solutions using Whatman #1 filter paper, and analyzed the extracts for NH_4^+ and NO_3^- colorimetrically using an Alpchem Autoanalyzer (College Station, TX).

Soil enzyme analysis was conducted using methods developed by Tabatabai (1982), as modified by Sinsabaugh et al. (1993) and Sinsabaugh and Findlay (1995). Acid phosphatase activities were determined using *p*-nitrophenol (*p*NP)–phosphate, and phenol oxidase activities were measured by oxidation of L-3,4-dihydroxyphenylalanine (L-DOPA) during 1 h incubations (Boerner et al., 2005).

2.4. Statistical analyses

All data were checked for homogeneity of variance in order to meet assumptions of parametric analysis. Those data that did not meet the assumptions were log-transformed prior to analysis. We tested for the effects of burn season treatment and year on soil environmental, biogeochemical, and microbiological variables at the experimental unit level using one-way ANOVAs with treatment (early season burn, late season burn, and control) and year (2002, 2003 and 2004) as the independent variables ($n = 3$). Significant differences between treatment means were determined using Tukey's highly significant difference (HSD) ($\alpha = 0.05$). We ran Pearson's correlations to examine the relationship between soil enzyme activity and soil environmental variables (soil H_2O, temperature, pH, total C and total N). We ran all analyses using the Statistical Analysis System (SAS Institute, 1997).

3. Results

3.1. Fire effects on soil environmental variables

There was no change in average soil moisture 1 year after the early season burn, relative to the control, but there was a 22% decrease in soil moisture 1 year after the late season burn, relative to the control. This difference in the late season burn treatment from the control was still evident, although less pronounced, 2 years post-fire (Fig. 1a). There was also a significant year effect on this parameter, reflecting an overall decrease in soil moisture from 2002 to 2004 ($p < 0.001$). Similarly, soil pH was not significantly different from the control after the early season burns, but there was a large increase in soil pH 1 year post-fire in the late season burn treatment, relative to the control (Fig. 1b). By 2004, however, soil pH levels in the late season treatment returned to unburned levels. There was also a significant year effect on soil pH ($p < 0.001$). Soil temperature (only measured in 2004) was significantly higher in both the early season and late season burn treatments than in the control (Fig. 2).

3.2. Fire effects on soil carbon and nitrogen pools

Early season burns did not significantly alter total soil carbon, relative to the control; however, soil carbon was 17% lower in the late season burn treatment than the control 1-year post-fire

Table 1
Characteristics of early and late season prescribed fires conducted in the Giant Forest region of Sequoia National Park, CA

	Scorch height (m)[a]	% Area burned[a]	% AG litter and duff consumed[b]	% Tree mortality (2002)[c]	% Tree mortality (2004)[d]
Early Season	11.1	70	66	26	38
Late Season	13.5	88	79	37	56

Treatment means are presented; AG = aboveground.
[a] Data from Knapp and Keeley (2006).
[b] Data from Knapp et al. (2005).
[c] Direct tree mortality from fire (Schwilk et al., 2006).
[d] Direct tree mortality from fire and post-fire mortality from bark beetle infestation (Schwilk et al., 2006).

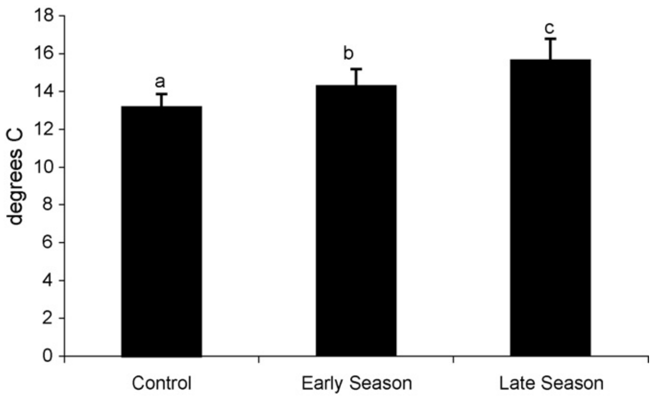

Fig. 2. Effects of early and late season fire on soil temperature two growing seasons post-fire (2004). Treatment means (+1 S.E.) are presented. Different letters denote a significant treatment difference ($p < 0.05$).

(Fig. 3a.). This effect of burn season continued into 2004 but differences diminished. We found no significant effect of either early season or late season burns on total soil nitrogen levels but we did see a significant year effect ($p < 0.001$), with 2002 being higher than both 2003 and 2004 (Fig. 3b).

The total inorganic nitrogen pools (TIN) increased significantly with both early season and late season burning, but the spike in the late season burn was nearly two and half times greater than the spike in the early season burn sites (Fig. 3c). This flush of available nitrogen was short-lived, however; concentrations returned to control levels by 2004 in all treatment plots.

3.3. Fire effects on soil carbon and nitrogen turnover rates

Soil respiration rates were significantly lower than the control 1-year post-fire in both the early season (28% lower) and late season (35% lower) burn treatments. This trend continued into 2004 (Fig. 4a). There was also a significant year effect ($p < 0.001$), indicating an overall increase in soil respiration rate in the control treatment from year 2002 to 2004. There was a dramatic shift in nitrogen dynamics in the control treatment from net mineralization in 2002 to net immobilization in 2003 and then back to net mineralization in 2004 (Fig. 4b), reflecting a significant year effect on this flux ($p < 0.001$). The early season burns significantly increased net nitrogen mineralization rates relative to the control 1-year post-fire but late season burns had no effect on the net nitrogen mineralization rates 1-year post-fire. By 2004 there was no significant difference in net nitrogen mineralization rates between the fire treatments and the control. Despite significant treatment and year differences, the net nitrogen mineralization rates were not significantly different from zero in years 2003 and 2004 (Fig. 4b).

3.4. Fire effects on soil microbial enzyme activity

Acid phosphatase, an enzyme often correlated with microbial biomass and nitrogen and phosphorus cycling (Clarholm, 1993; Decker et al., 1999; Boerner et al., 2000), was significantly lower in both early and late season burn treatments than the unburned control in 2004 (Fig. 5). Phenol oxidase, an enzyme responsible for the degradation of lignin (Carlisle and Watkinson, 1994; Boerner

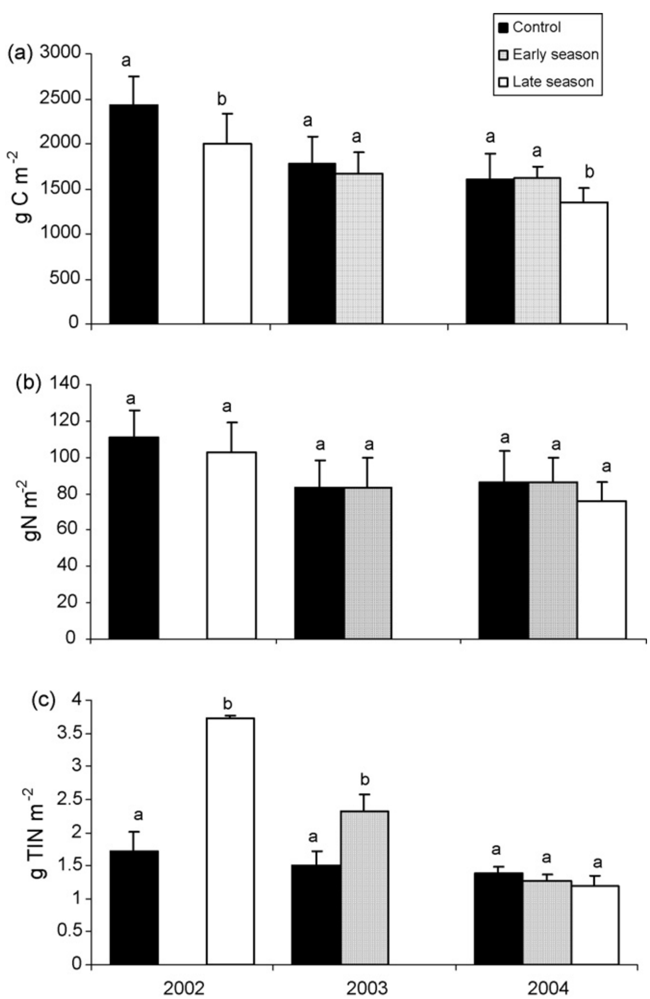

Fig. 3. Treatment effects on total soil carbon (a), total soil nitrogen (b) and total inorganic nitrogen (TIN) (c). Treatment means (+1 S.E.) are presented. Within-year treatment differences ($p < 0.05$) are represented by different letters.

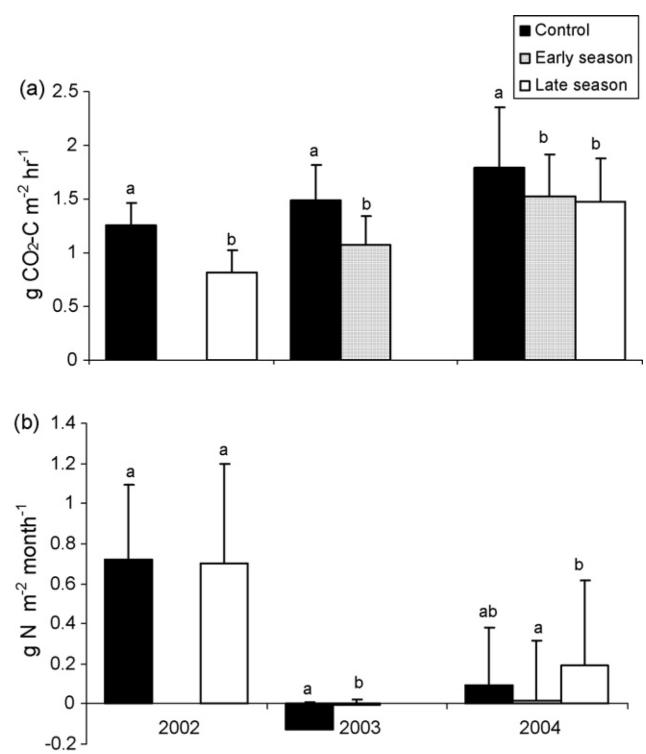

Fig. 4. Treatment effects on soil respiration rates (a) and net nitrogen mineralization rates (b). Treatment means (+1 S.E.) are presented. Within-year treatment differences ($p < 0.05$) are represented by different letters.

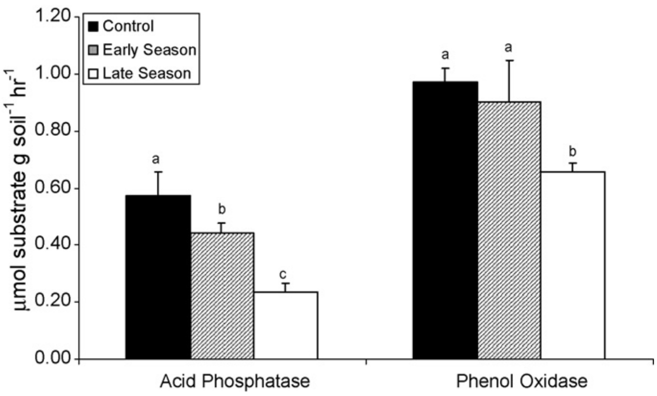

Fig. 5. Season of burning impact on soil enzyme activity as measured by the amount of substrate consumed by the enzyme during a 1-h incubation. Results are from two growing seasons post-fire (2004). Treatment means (+1 S.E.) for each enzyme are displayed with a significant difference of $p < 0.05$ represented by different letters.

et al., 2000), showed no significant difference in activity with early season fire, but had significantly lower activity with late season burning (Fig. 5). In order to assess how microbial activity varied in relation to soil environmental conditions in fire-affected soils, we ran correlations between enzyme activity and all soil environmental variables. Acid phosphatase activity was positively correlated with soil moisture, total soil C, total N, and total inorganic N and negatively correlated with soil pH and temperature (Table 2). Phenol oxidase activity was weakly, but significantly correlated with soil temperature and total inorganic N.

4. Discussion

Late season burns had a much more dramatic effect on soils than early season burns. Significant differences in soil moisture, soil pH, soil C, and soil N were found between the late season burn treatment and the control 1-year post-fire. None of these variables differed from the control in the early season burn treatment. This suggests that the combined effects of temperature, moisture, and duration of heating during the early season burns were not intense enough to alter the physical and chemical properties of the litter and soil. Late season burns consumed 88% (158.9 mg/ha) of the available fuels, while early season burns consumed only 67% (121.6 mg/ha) of the available fuels (Knapp et al., 2005). In addition, studies have shown that the heat produced by combustion penetrates less deeply into the soil when soils are moister (Hartford and Frandson, 1992; Campbell et al., 1994; Giovannini and Lucchesi, 1997; Busse et al., 2005), because water absorbs a considerable amount of heat energy. Different soil water content at the time of fire can significantly alter fire effects on microbial populations (Dunn et al., 1985) and nutrient transformations (Choromanska and DeLuca, 2002). Soils were substantially moister at the time of the early season burns (Knapp, personal observation), although only duff moisture was actually measured. Because duff is in direct contact with the soil and loses moisture as the soil dries, duff moisture should be roughly proportional to soil moisture. Duff moisture averaged 29 and 11% during the early and late season burns, respectively (Knapp et al., 2005).

The short-term decrease in post-burn soil moisture in the late season burn treatment was likely due to several mechanisms. First, the vaporization of hydrophobic hydrocarbons in the litter during fire and the subsequent condensation of these compounds on soil aggregates deeper in the soil profile can create hydrophobic patches in soil (Neary et al., 1999; DeBano and Neary, 2005). This phenomenon has been shown to be a primary cause of post-fire increases in runoff and erosion in moderate to high severity burn sites (Huffman et al., 2001; Robichaud, 2000; Benavides-Solorio and MacDonald, 2005; Carroll et al., 2007). A separate study at nearby sites in Sequoia National Park found that runoff coefficients were elevated 7–35% above pre-fire levels for 9 years after fire (Engle et al., 2008). Lower post-burn soil moisture in our sites could also be attributed to higher soil temperatures, likely due to decreased albedo, and the loss of the insulating litter layer.

Fire intensity also likely played a large role in altering soil pH levels. Higher fire intensity in the late season burns presumably caused greater rates of combustion of un-dissociated organic acids in the litter and soil, removing them from the system. Also, the leaching of alkaline metals from the ash into the soil complex and the associated consumption of hydrogen ions in the formation of water could have led to higher pH levels in the late season burn sites (Neary et al., 1999). Changes in soil pH have been correlated with soil microbial community structure (Fierer and Jackson, 2006). By selecting against certain functional groups that favor lower pH levels (namely, fungi), disturbances such as fire may have short- and long-term impacts on C turnover rates and storage in the soil (Bailey et al., 2002).

There was a decrease in soil C with late season burning, relative to the controls, which persisted throughout the study. This likely reflects the higher severity of these burns. The persistence of this condition 3 years post-fire suggests that there was slow recovery of the above and belowground biota in these sites. Within each year, there was no effect of treatment on total soil nitrogen. The influence of fire on total soil N pools has been controversial in the literature; with some studies reporting an increase (Covington and Sackett, 1992; Kovacic et al., 1986; Schoch and Binkley, 1986), others a decrease (Bell and Binkley, 1989; Raison et al., 1985), and some showing no change (Knoepp and Swank, 1995; Moghaddas and Stephens, 2007) in total soil nitrogen pools after fire. This inconsistency in the published literature is likely due to the complex nature of factors influencing nitrogen pools (soil moisture, leaching, soil erosion, plant uptake and microbial immobilization), the spatial heterogeneity of the nitrogen loss during fire, and the soil depth sampled. Depending on intensity, the effects of fire are typically diminished below 5 cm (Neary et al., 1999), so if soils are sampled below this depth and mixed, as they were in this study, the effect of the burn may be diluted by the unaffected deeper soil horizons (Gillon and Rapp, 1989; Wan et al., 2001).

The response of the inorganic nitrogen pool to the different fires agrees with many other studies, showing an initial increase in the available nitrogen after low- to moderate-severity fire (Covington and Sackett, 1992; Gundale et al., 2005; Moghaddas and Stephens, 2007). This pulse of available nitrogen can last several months to

Table 2
Correlations between soil enzymes and environmental variables for year 2004

	H_2O (g kg^{-1})	Temperature (°C)	pH	C (g kg^{-1})	N (g kg^{-1})	TIN (g kg^{-1})
Acid phosphatase	0.44*	−0.55*	−0.44*	0.54*	0.44*	0.49*
Phenol oxidase	0.25	0.35*	0.18	0.02	0.06	0.29*

Pearson's correlation coefficients are presented, with significance of $p < 0.01$ designated by an asterisk (*).

several years, depending on the vegetative recovery and the regional climate. Because the burns in this study were all low- to moderate-intensity, they were not intense enough to volatilize a large portion of the system nitrogen. Also, Knapp et al. (2007) documented an increase in N-fixing *Ceonothus* sp. post-fire in these plots, partially contributing to the initial increase in available nitrogen.

The significant drop in soil respiration with both early and late season burning 1 and 2 years post-fire can be partially explained by tree mortality; mean tree basal area decreased approximately 15.8% in early season burn treatment and approximately 17.2% in the late season burn treatment (Schwilk et al., 2006), decreasing the autotrophic contribution to total respiration. The majority of this mortality was in the saplings and small diameter trees, causing a shift in the tree size distribution towards larger size classes in the burned sites (Schwilk et al., 2006). There was likely an immediate drop in heterotrophic contribution as well, with direct mortality of soil organisms during the fire and indirect impacts on heterotrophic activity by altered environmental conditions post-fire. Understanding how these different soil components respond to different fire applications will aid us in building belowground carbon budgets for forest systems that experience frequent fires.

The changes we saw in the net nitrogen mineralization rates were not consistent with most studies showing a short-term increase in nitrogen turnover rates post-fire (Hobbs and Schimel, 1984; Schoch and Binkley, 1986; Kaye and Hart, 1998; DeLuca and Zouhar, 2000). However, our results agree with other FFS studies (Miesel et al., 2007; Moghaddas and Stephens, 2007) that reported a significant increase in mineral soil inorganic nitrogen concentrations, but no effect of fire on net mineralization rates. Through root death, the late season fires may have provided a flush of carbon substrate to the microbial populations, stimulating microbial immobilization rates and temporarily reducing the net mineralization rates to control levels. Alternatively, the reduction of labile C pools in the top few centimeters of soil post-fire may have limited C availability to the heterotrophic microbes, temporarily decreasing mineralization rates. By the time we sampled the burn units again in 2004, the net rates were not significantly different from those in the control and the initial increase in the early season burn treatment (relative to the control) had subsided. These results may also be attributed to methodology: we used the soil core incubation method. One artifact of this method is that core placement usually involves the severing of roots. The dead and dying roots inside the soil core provide a flush of organic substrate for the microbial population, potentially leading to increased immobilization rates (Adams et al., 1989; Hook and Burke, 1995), and, subsequently, lower net mineralization rates.

Decomposition rates are jointly controlled by soil microclimate and by activities of cellulose and lignin-degrading extracellular enzymes (Sinsabaugh et al., 1992). Inside microbial cells, enzyme production is regulated by moisture, temperature, pH, and nutrient availability. Once enzymes are released into the soil solution, however, their activity is limited by substrate chemistry and availability (Sinsabaugh et al., 1992; Waldrop et al., 2004). Large changes to either environmental conditions or substrate chemistry could therefore significantly alter microbial enzyme activity and, hence, decomposition rates. Previous work has shown that acid phosphatase activity is highest at low soil pH (5–5.5) (Saa et al., 1993; Staddon et al., 1998; Acosta-Martínez and Tabatabai, 2000), so the fire-induced increase in pH in 2002 may have limited subsequent acid phosphatase activity in these units. Clarholm (1993) has shown that elevated available soil P, which has been found in fire-affected soils in the Sierra Nevada (Murphy et al., 2006), reduces acid phosphatase activity by reducing the need for microbial expenditure of the enzyme. Our results agree with several studies that have reported reduced acid phosphatase activity in forest (Staddon et al., 1998; Boerner et al., 2000; Miesel et al., 2007) and shrubland (Saa et al., 1993) soils after fire.

Eivazi and Bayan (1996) found that frequent burning caused greater reductions in both acid phosphatase and phenol oxidase than less frequent burning. Because phenol oxidase targets older litter that is rich in lignin, it is not typically active in early stages of decomposition with fresh litter (Carlisle and Watkinson, 1994; Waldrop et al., 2003). The lack of sufficient older substrate in the late season burn treatment may have led to reduced phenol oxidase activity. The less severe early season burns did not impact phenol oxidase activity. Boerner et al. (2000) and Giai and Boerner (2007) also found that low-severity fire had either no impact or a positive impact on phenol oxidase activity, suggesting that the fire did not dramatically change the composition of the organic matter complex within the soil.

Both the changes in soil environmental conditions and the associated drop in soil enzyme activity are consistent with the higher severity of the late season burns. The fact that soil enzyme activity had not returned to pre-fire levels within 2–3 years suggests that either overall microbial activity was still lower than in unburned sites or that different enzymes were at work in the fire-affected sites. Fire-affected shifts in microbial structural and functional diversity have been found elsewhere (Bååth et al., 1995; Giai and Boerner, 2007; Hamman et al., 2007), suggesting a disturbance-induced change in substrate quality. Analyzing a suite of microbial enzymes that target several different types of carbon substrate and that are active under variable environmental conditions can provide a estimate of fire effects on microbial activity and a glimpse into the belowground functional changes that occur with disturbances such as fire.

Because the 2004 measurements were completed 26 months after the early season burns and 34 months after the late season burns, the late season burn units had a longer time to recover. The fact that the late season burn treatment continued to show greater change from the control suggests that the difference between the two fire season treatments in soil moisture, temperature, total carbon, and microbial enzyme activities may actually be greater than what is shown by the 2004 data. Results of this study must also be seen in light of the biotic and abiotic conditions at the time of the burns. While the conditions were typical for early and late season prescribed burns in this forest type, results might be different if, for example, early season burns had been conducted after a dry spring, if the late season burns had been conducted after the soils had been moistened by earlier rains, or if fuel loads were closer to historic levels.

The significant year effect in all measured variables suggests that there may be a large climatological influence on these ecosystem parameters. Total annual precipitation in the study area in 2002 (209 cm) was two times higher than in 2003 (106 cm) and nearly 2.5 times higher than 2004 (83 cm) (National Climate Data Center, http://cdo.ncdc.noaa.gov). Most of the precipitation in this system falls as snow and vegetation capitalizes on spring runoff from snow melt. The drop in precipitation in 2003 and 2004 may have limited both above and belowground productivity, altering several soil parameters (especially total soil N and net N mineralization) in the treated and control sites during the time of the study, overriding any treatment effect.

5. Conclusions

The decision to burn in the spring or the fall is influenced by several ecological, climatological, social, and political factors. The study area, like many forest ecosystems of the western United

States, has had a long history of frequent low to moderate intensity late season fire, which had been interrupted by modern policies of fire suppression. Removing the fuel that has accumulated without adversely impacting the ecosystem properties and processes remains a management challenge. High fire intensities resulting from the consumption of unnaturally high fuel loads could negatively affect soil properties. Burns conducted under higher fuel moisture conditions, such as those commonly found in the early season, consume less fuel (Knapp et al., 2005), potentially reducing fire intensity. However, because historic fires rarely burned at this time of year, early season burns may also have unwanted consequences if important soil biotic and abiotic variables are altered to the detriment of the ecosystem. Results from this study showed that for soil variables differentially affected by burning season, the magnitude was nearly always greater with the late season burns than early season burns. For several of these variables the effect was transient, however, and significant only in the first year after the burns.

Our finding that the response of soil variables to early season prescribed burns was often intermediate to the response to late season burns and the unburned control is in line with results previously reported for other ecosystem components including trees (Schwilk et al., 2006), understory vegetation (Knapp et al., 2007), and forest arthropods (Ferrenberg et al., 2006). For many of these variables, the differential response to burning season was thought to have been due to greater fuel consumption and fire intensity of the late season burns. This suggests that much like the aboveground ecological variables, soil variables may be regulated more strongly by fire severity than by the season in which the prescribed fire is conducted.

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